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Ecological and social effects on reproduction and local recruitment in the red-backed shrike

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Abstract Numerous hypotheses have been proposed to explain variation in reproductive performance and local recruitment of animals. While most studies have examined the influence of one or a few social and ecological factors on fitness traits, comprehensive analyses jointly testing the relative importance of each of many factors are rare. We investigated how a multitude of environmental and social conditions simultaneously affected reproductive performance and local recruitment of the red-backed shrike *Lanius collurio* (L.). Specifically, we tested hypotheses relating to timing of breeding, parental quality, nest predation, nest site selection, territory quality, intraspecific density and weather. Using model selection procedures, predictions of each hypothesis were first analysed separately, before a full model was constructed including variables selected in the single-hypothesis tests. From 1988 to 1992, 50% of 332 first clutches produced at least one fledgling, while 38.7% of 111 replacement clutches were successful. Timing of breeding, nest site selection, predation pressure, territory quality and intraspecific density influenced nest success in the single-hypothesis tests. The full model revealed that nest success was negatively associated with laying date, intraspecific density, and year, while nest success increased with nest concealment. Number of fledglings per successful nest was only influenced by nest concealment: better-camouflaged nests produced more fledglings. Probability of local recruitment was related to timing of breeding, parental quality and territory quality in the single-hypothesis tests. The full models confirmed the important role of territory quality for recruitment probability. Our results suggest that reproductive performance, and particularly nest success, of the red-backed shrike is primarily affected by timing of breeding, nest site selection, and intraspecific density. This study highlights the importance of considering many factors at the same time, when trying to evaluate their relative contributions to fitness and life history evolution.

Keywords Timing of breeding · Nest site selection · Intraspecific density · Predation · Territory quality

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Introduction

Reproductive performance and recruitment are key components of individual fitness (Futuyma 1990). Numerous studies have focused on the importance of single ecological or social factors for reproductive performance and/or recruitment (for reviews see Clutton-Brock 1988; Newton 1989). Far less common, however, are comprehensive studies examining how a multitude of factors may simultaneously influence reproduction and recruitment (Krüger 2002). Such studies are important because they can help to disentangle the relative impact of various factors on fitness. Furthermore, reproductive decisions in animals are shaped by natural selection in response to the entire environment in which they live, and this environment includes such differing features as, for example, predation, weather conditions and mate age.

Here, we examine what factors affect reproductive performance and local recruitment in the red-backed shrike (*Lanius collurio* L.) living in a sub-alpine environment 1,100–1,700 m above sea level (a.s.l.). The

red-backed shrike is a trans-Saharan migratory bird species that returns to the breeding grounds in mid-April to early June and settles in habitats with meadows and pastures containing shrubs and trees, where the birds build open-cup nests. We analyse data covering 5 years and including more than 480 clutches from a densely populated study site of roughly 2 km^2 in the Swiss Alps.

The major hypotheses put forward to explain variation in reproductive output and recruitment in seasonally breeding birds relate to timing of breeding, parental quality, predation, nest site selection, territory quality, intraspecific density and weather. In the following, we will briefly review these hypotheses and derive predictions relevant to the red-backed shrike. These predictions are then first examined in separate analyses. Based on these results, we investigate how multiple factors simultaneously act on: (1) nest success and number of fledglings (reproductive performance) and (2) the probability that a nest produces at least one offspring surviving to breed in the study area (local recruitment). This approach allows us to test the relative contribution of variables referring to different hypotheses.

Hypotheses and predictions

The timing-of-breeding hypothesis proposes that birds breeding early in the season realize highest fitness by producing more fledglings and more recruits (Wheelwright et al. 2003; but see Monros et al. 2002). We therefore predict a seasonal decline in reproductive performance and local recruitment in red-backed shrikes (Electronic supplementary material S1, prediction 1a). Since we studied red-backed shrikes over an altitudinal gradient of 600 m, a second prediction (S1, prediction 1b) is that the seasonal decline of reproductive success and local recruitment is more pronounced with increasing altitude, which decreases the length of the breeding season.

Parental quality may affect reproduction and local recruitment via at least two pathways. First, the age of the parents has been shown to influence reproductive success in a variety of species, with older birds generally reproducing more successfully than younger individuals (e.g. Forslund and Pärt 1995; Schiegg et al. 2002). Under this scenario, we expect reproductive performance and local recruitment to increase with parental age (S1, prediction 2a). Secondly, differences in condition or quality among individuals, independent of age, may account for variation in reproductive performance and local recruitment (Wheelwright et al. 2003). In this case, we predict that reproductive performance and local recruitment are positively associated with individual quality (other than age) (S1, prediction 2b).

Nest predation is a major source of nest losses in a variety of bird species and is therefore considered to be one of the driving factors of life history evolution (Martin 1995). On average, predation on open-nesting songbird nests accounts for 50–80% of the annual nest losses (Best and Stauffer 1980), with extreme values ranging from 0 to 100% (Hoover et al. 1995). There is evidence that the predation rate increases with density of predator species (De Santo and Willson 2001). We therefore predict that reproductive performance and/or local recruitment in the red-backed shrike is negatively related to predation risk (S1, prediction 3a), measured through predator density and the distances of nests to the nearest forest and human settlement.

As predation is the main cause of nest failure in many bird species, predation pressure should be a major factor determining nest site selection (Rauter et al. 2002). Among the many factors potentially influencing nest site selection, several structural characteristics of the immediate nest environment have been found to be important predictors of nest success. Nest concealment is generally thought to increase nest success and/or fledgling production in open-nesting species (Weidinger 2002; but see Howlett and Stutchbury 1996), so a first prediction of the nest habitat hypothesis is that nest concealment and reproductive performance are positively associated (S1, prediction 4a). Height of a nest above ground has also been shown to affect nest success in open-nesting species. Nests appear to be most successful if they are placed at some intermediate height relative to the range of realized nest heights in a particular species (Schäfer 2002). Nests placed close to the ground usually suffer increased predation from mammalian predators and nests located high above ground are more likely to be lost to avian predators (Schäfer 2002). A second prediction in relation to the nest site hypothesis is therefore that reproductive performance should be highest for nests built at an intermediate level of species-specific nest heights (S1, prediction 4b). Apart from nest concealment and nest height, nest site selection includes the structures onto which the nest is built. In shrikes, nests are usually built in shrubs and trees, but the consequences of substrate type for nest success are equivocal. Some studies have found higher reproductive output for nests placed in thorny shrubs compared to nests in shrubs without thorns (Tryjanowski and Kuzniak 1999); in turn, other studies reported higher reproductive success in coniferous than in deciduous trees, but found no difference between nests in thorny and thorn-less shrubs (Jakober and Stauber 1981, 1987; Farkas et al. 1997). Thus, as a third prediction of the nest site selection hypothesis, reproductive performance is expected to differ in response to shrub and tree type used as nest carrier (S1, predictions 4c and 4d).

Territory quality has been shown to be an important factor influencing reproductive success and recruitment in birds (Breininger and Carter 2003; Penteriani et al. 2003), with high-quality territories conferring fitness advantages. We therefore predict that reproductive performance and local recruitment are positively related to the quality of territories (S1, prediction 5a), measured on the basis of several structural habitat variables.

Density dependence is considered to be a central mechanism underlying the regulation of populations

(Newton 1998). Numerous studies have shown that reproduction and recruitment can be negatively affected by conspecific density (e.g. Forrester 1995; Newton 1998). We therefore predict that we will find a negative relationship between density estimates of the red-backed shrike and reproductive performance and local recruitment (S1, prediction 6a).

On the other hand, density-independent factors such as weather conditions during incubation and/or the nestling and post-fledging periods may have severe impacts on the reproductive performance of individuals, and may thereby account for much of the variation in reproductive output among individuals and populations (Krüger 2002; Rodriguez and Bustamante 2003). Inclement weather generally reduces reproductive success and recruitment, and such relationships may be accentuated at higher elevations, as for example in our study site. We therefore expect to find a relationship between weather conditions during the breeding season and reproductive performance and local recruitment, with warm and dry weather conditions being advantageous (S1, prediction 7a).

Materials and methods

Study area

The study was carried out in the Engadin, an alpine valley in eastern Switzerland (46°50'N/10°23'E). The Engadin is one of the strongholds of the red-backed shrike in Switzerland, with densities of up to 5.4 breeding pairs per 10 ha (Müller and Leugger 1998). The study site of 192.5 ha extended from 1,090 to 1,680 m a.s.l. and consisted mainly of steep slopes (inclination up to 40%) and of a few level parts at lower altitudes. The study site bordered on spruce (*Picea abies* Karst.) and pine (*Pinus* sp.) forests and, to a lesser extent, on grey alder (*Alnus incana* Moench) forests, the river Inn and a ravine. Hay meadows and pastures covered most of the study area. During the study period, agricultural practices were low intensity: hay meadows were usually cut once (on the steep slopes) or twice, and silage was conducted only on 4 ha. Structural diversity of the study area was remarkable, with an average hedge density of 12 km km^{-2} as compared to 1.1 km km^{-2} in the Swiss lowlands (Kohli and Birrer 2003). Orchards and single trees added to the structural diversity, particularly close to villages.

Field methods

Data were collected from 1988 to 1992. Observations started in mid-March and lasted until the end of August, the exception being 1988, when data were collected from early May to the end of July. In March, April and early May, the study area was visited once, twice and four times a week, respectively, while after mid-May, the study area was frequented daily.

Most red-backed shrike nests were found during egg laying, but nest checks were, with a few exceptions, postponed to the nestling period to minimize disturbance. As soon as adults were observed feeding, age of the nestlings was estimated based on comparisons with reference nests that had been visited daily. An effort was made to ring nestlings of all clutches on day 8 (day 1 = hatch date). Age of nestlings was then verified on the basis of body mass (to nearest 0.5 g) and length of third outermost primary (to the nearest 0.1 mm), again by comparing with reference nests. Each nestling was marked with a coloured, numbered aluminium band, with different colours each year.

Adults were mainly caught during the nestling period with a mist net placed close to the nest; these birds were individually banded with two coloured aluminium bands, each band bearing two colours to increase individual combinations. The following measurements were taken from each adult: body mass (to nearest 0.5 g) and length of third outermost primary (to nearest 0.5 mm), hereafter referred to as primary length. Adults were aged based on their banding history, i.e. individuals banded as nestlings and recaptured 1 year later were classified as 1-year-old birds, individuals captured for the first time were considered to be at least 1 year old, and individuals banded as 1-year-olds and observed again in the next year(s) were classified as being at least 2-year-old birds, etc. Because nestlings had not been colour-banded individually, all birds marked as nestlings that returned to the study area were captured for identification from the numbered aluminium band. This allowed us to assess local recruitment rate for each nest.

Variables used to test hypotheses on reproductive performance

Unless stated otherwise, year was included as a continuous variable in all analyses relating to reproductive performance to account for annual differences, and we do not specifically point this out in the following sections.

Timing of breeding and altitude

Hypotheses pertaining to timing of breeding were examined using laying date (continuous variable) and clutch sequence (categorical variable with two levels: first or replacement clutch). Based on the age of nestlings, laying date of the first egg was calculated by backdating, assuming that one egg was laid per day, that incubation started with the penultimate egg in a clutch (57.7% of all nests had a runt; M. Müller, unpublished data) and that the interval between incubation start and hatching of the first egg was 15 days (based on own data and Glutz von Blotzheim and Bauer 1993). Laying date was then expressed as day relative to 1 May (1 May = day 1; 31 May = day 31, etc.).

Red-backed shrikes usually raise only one successful brood (Glutz von Blotzheim and Bauer 1993). Out of 489

clutches, only one pair managed to successfully raise two broods in our study area. If the first attempt fails, a replacement clutch is usually produced. Accordingly, each nest was classified either as first brood (first breeding attempt of a pair) or as replacement brood (subsequent breeding attempt of the same female after loss of first brood). The successful second brood mentioned above was excluded from the analyses. Altitude was entered as elevation of the nest site in km a.s.l. (continuous variable).

Parental quality

Parental quality was estimated through variables referring to age, size and condition of the breeding birds. Age effects were analysed with a categorical variable with three levels. Adults were classified as being: (1) 1 year old if ringed as nestlings in the previous year; (2) > 1 year old if resighted in a year following first capture as adults; and (3) unknown if captured first as unringed adults. Primary length was used to account for differences in body size and body mass to reflect variation in parental body condition. Body condition was measured as the residuals of a multiple regression of body mass on age of nestlings at the time of capture, body size (i.e. primary length), time of day and year of capture, to account for potential bias arising through these factors. Only data from the first capture of each individual were used in these analyses, i.e. each individual was considered only once. Body size and condition were both treated as continuous variables.

Nest predation

To estimate the potential impact of corvid predation on red-backed shrike reproductive performance, the annual number of territories of jays (*Garrulus glandarius* L.), magpies (*Pica pica* L.), and carrion crows (*Corvus corone* L.) in the entire study area was used in the analyses. Since these variables were highly intercorrelated, they were reduced to two factors by principal component analysis with varimax rotation to optimize factors. Factor 1 represented territory numbers of magpies [$\log(x+1)$ transformed to achieve normal distribution] and carrion crows (hereafter referred to as magpie/crow factor), while factor 2 was related to the number of jay territories (hereafter referred to as jay factor). Both factors explained 92.5% ($n = 380$) of the variance in territory number of these three species. To examine the influence of forest-living predators or those associated with human settlement, such as cats, we also included the distances from the nest to the nearest forest and human settlement. All variables in these analyses were entered as continuous variables.

Nest site

To describe the nest site, four variables were used. Nest concealment, the first variable, was visually estimated from five directions during the first nest check, the directions being below and above the nest, when standing in front of the nest (defined as the side allowing easiest access to the nest, usually the side with the shortest distance to the edge of the nest hedge/bush), when standing behind the nest (the opposite side of the nest carrier, based on the front position), and the side of the nest (defined as the side with the least concealment and being perpendicular to the line between front and behind positions). For each of these five directions, nest cover was then scored with three classes: 0 = visibility of the nest < 10%; 1 = visibility 10–50%; and 2 = visibility > 50%. Visibility was estimated from a distance of 1 m from the bush or hedge containing the nest. Then, for each nest, the sum over all five directions was calculated, giving a minimum of 0 for well-concealed nests and a maximum of 10 for highly visible nests. After fledging of the young, three further parameters were recorded for each nest: height above ground (m), location (four categories: bush, hedge, single tree/tree group, and forest edge), and substrate type carrying the nest (two categories: with or without thorns, cf. Tryjanowski et al. 2000). All variables were treated as continuous variables except for nest location and substrate type.

Territory quality

Territory quality was measured using eight variables referring to habitat structures relevant to the ecology of red-backed shrikes (Glutz von Blotzheim and Bauer 1993; Leugger-Eggimann 1997; M. Müller, unpublished data). For each territory, the percentage cover of meadows managed at (1) low and (2) high intensity, (3) dry meadows, (4) arable land (acres) and (5) unmanaged areas was estimated, as well as (6) the length (m) of hedges and (7) the number of free standing bushes and (8) of trees. Of these eight variables, high values for variables (2) and (4) were considered to reflect low-quality territories, while high values for the other six variables were considered indicative of high territory quality. Territory boundaries were determined by connecting the outermost observations of territorial disputes and foraging (10–20 per male). Several territories were occupied in more than one year, in which case we randomly selected one year for each territory to use in the analyses. Intercorrelations among territory quality variables were low except for meadows managed at low intensity, which were negatively correlated with dry meadows and with meadows managed at high intensity (Spearman rank correlation $r_s = -0.56$ and -0.53, respectively, $n = 118$, $P < 0.001$). We therefore excluded the variable referring to meadows managed at low intensity from the analyses to avoid problems of multicollinearity in the multivariate analyses (Chatterjee and Price 1991). As an additional measure of territory quality, we included occupation frequency of a territory, which was calculated as the number of years a territory had been occupied by breeding pairs or solitary males during the study period (ranging from 0 to 5 years). All variables were treated as continuous variables.

Intraspecific density

As measures of intraspecific density, we used the number of territories (with breeding pairs or unpaired males) of red-backed shrikes within 150 m of the focal nest, the distance (m) to the nearest nest of red-backed shrikes and the total number of red-backed shrike territories within the study area in a given year (hereafter referred to as population density). All measures were entered as continuous variables.

Weather

We used daily mean and minimum temperature (°C), total number of hours with sunshine, amount of rainfall (mm) during daytime (between 7:00 a.m. and 7:00 p.m.) and at night (between 7:00 p.m. and 7:00 a.m. of the following day) as weather measures. Data were obtained from the SMI-MeteoSwiss station in Scoul (1,280 m a.s.l.) located about 8.5 km northwest of the study area. For each variable, we calculated mean values for each nest separately over 15 days following the onset of incubation. This timespan reflects the incubation period (see above). Next, we calculated means over the 15 days following the hatching date, which allowed us to analyse nest losses in the egg and nestling stage separately, as well as for the combined incubation and nestling periods. We decided to use the data referring to incubation period, because several nests were depredated during the egg stage, making a reference to weather during the nestling period questionable. Results did not change, however, if we considered the nestling period only or the combined incubation and nestling period (data not shown). Weather variables were highly intercorrelated and were hence reduced to two factors by principal component analysis using varimax rotation. Factor 1 represents temperature (i.e. sunshine, mean and minimum temperature) and factor 2 stands for rainfall (i.e. amount of rain in the day and during the night): both factors together explained 85.5% of the variance in the data set ($n = 443$). Both factors were treated as continuous variables. Since the temperature factor was highly correlated with the laying date ($r_s = 0.88$, $P < 0.001$, $n = 443$), which in turn we hypothesized would influence reproductive success, we created a variable measuring reproductive success independent of laying date. This was achieved by regressing nest success and number of fledglings from successful nests on laying date, and using the residuals of these regressions as dependent variables in the subsequent analyses referring to weather.

Variables used to test hypotheses on local recruitment

Most variables used were identical to those just described for analysing reproductive performance. However, since the analysis of local recruitment focuses on the period after fledging, we included some additional variables referring to that period and, in turn, excluded some variables referring to the incubation and nestling stage only. The influence of timing of breeding on local recruitment was again examined with the variables laying date, altitude a.s.l. and year. Predictions derived from the parental quality hypothesis were tested with the variables age, body size and body condition (see above for definitions and calculations). The nest predation hypothesis was investigated with the magpie/crow factor and the jay factor as well as the nearest distances to human settlement and forest. We did not test variables referring to the nest site selection hypothesis because these parameters bear no relationship to the fledged young moving around in the parental territory. To test for an effect of territory quality on recruitment probability, we included the variables referring to habitat structure and occupation frequency of a territory. The influence of intraspecific density was examined with the annual number of shrike territories within the study area, while the two variables referring to the nest, i.e. conspecific density within 150 m of the nest and distance to the nearest nest, were not considered. Weather effects were investigated based on variables referring to the first 14 days after fledging. Averages over that period were first calculated from the original variables (amount of rainfall during daytime and at night, daily mean and minimum temperature, and total number of hours with sunshine). As in the analysis of reproductive performance, these averages were then subjected to principal component analysis with varimax rotation, and the two resulting factors, representing temperature and rainfall, explained 87.4% of the variation in the data set ($n = 370$). Fledging was assumed to occur 30 days after the onset of incubation (Glutz von Blotzheim and Bauer 1993).

Since nests with many fledglings may be more likely to produce a local recruit than nests with one or only a few fledglings, we included the number of fledglings per nest as a continuous variable in all analyses focusing on the probability of local recruitment (i.e. whether or not a nest produced a local recruit). This enabled us to examine the influence of the different variables on recruitment probability, while simultaneously accounting for differences in fledgling numbers.

Finally, we examined two variables relating ''quality'' of nestlings to recruitment probability. Body size and body condition of nestlings were measured as the residuals of multiple regressions of primary length and body mass on age, laying date and number of siblings.

Statistical analyses

Reproductive performance

We used nest success and number of fledglings from successful nests as measures of reproductive performance. Nests were considered successful if they produced at least one fledgling. Nest success was analysed by logistic regression (binary dependent

variable, success yes/no) using PROC LOGISTIC (SAS Institute Inc. 1999–2001), and number of fledglings by generalized linear models using a log link and assuming Poisson distribution (PROC GENMOD, SAS Institute Inc. 1999–2001). Only one randomly selected entry per breeding pair and year was included, but data from the same individuals from consecutive years were considered to be independent, because ecological and social circumstances in the study site varied annually.

Each hypothesis was first examined separately, including all variables needed to test the predictions of the hypothesis in question (S1). We fitted several models for each hypothesis using all possible combinations of the predictor variables, but only models that significantly explained variation in the data set [log likelihood ratio tests for nested models, $P < 0.05$ after Self and Lian (1987)] were included in the model selection process. Best models were then selected for each hypothesis using Akaike's Information Criterion (AIC; Akaike 1973; Burnham and Anderson 1998) corrected for small sample sizes (AICc; Burnham and Anderson 1998). Model fit was checked using residual analyses (McCullagh and Nelder 1989); multicollinearity was examined using tolerance values (Allison 2001).

Models with ΔAICc < 2 compared to the model with the lowest AICc were selected. The model with the lowest AICc value can be viewed as the most parsimonious one, i.e. the one explaining most of the variance with the fewest parameters (Burnham and Anderson 1998, 2001; Anderson et al. 2000). We then calculated Akaike model weights (Burnham and Anderson 1998) to determine the degree to which a selected model is supported by the data. Weights of selected models sum up to unity by definition, and higher weights indicate better explanatory power. Effect sizes of parameters of the selected models were calculated using model averaging: parameter estimates are multiplied by the weight of the particular model and summed over all selected models that contain the particular parameter to give the weighted average of parameter estimates (Burnham and Anderson 1998; Johnson and Omland 2004). Similarly, standard errors (SEs) were calculated for parameter estimates following Burnham and Anderson (1998). When describing effect sizes in the Results section, we present these weighted averages and SEs calculated from the selected models.

In a second step, the final predictors of these best models were used to build a comprehensive model to explain variation in reproductive performance under simultaneous consideration of multiple factors, using the same procedure as just described.

Recruitment

We proceeded as described for reproductive performance to test the hypotheses relating to recruitment. Factors influencing local recruitment were related to the probability that a nest produced at least one local recruit (dependent variable: yes/no) using logistic regression. Because recruitment rate was low (see Results section) and our data set hence unbalanced, we created new data sets containing a randomly selected subsample of fledglings not returning to the study area and of nests not producing recruits, with the random subsample being equal in size to the number of observations where recruitment occurred. This process was replicated 10 times and all analyses were repeated on these 10 data sets. To test whether individual quality (i.e. body size or condition) of a fledgling influences its recruitment probability, we created a data set containing fledglings that returned to the study area to breed (i.e. local recruits, $n = 34$) and fledglings which did not return. For the latter subset, we only used nests that had not produced local recruits to avoid including young from the same nest in the data set. The remaining multiple entries of the same nest (i.e. when a nest produced more than one recruit) were then removed by randomly selecting one individual per nest. Recruitment status (yes/no) was used as the dependent variable in a logistic regression. Data from 1992 were excluded from all recruitment analyses because the fate of individuals was not followed in 1993 and subsequent years. Only successful nests were included in all analyses concerning local recruitment.

Results

General findings

From 1988 to 1992, the number of breeding pairs remained stable, averaging 4.0 ($\pm$0.7 SD) breeding pairs per 10 ha, while the percentage of successful nests declined (see Fig. 1a, b). Fifty percent of 332 first clutches produced at least one fledgling, while 38.7% of 111 replacement clutches were successful. The mean number of fledglings was 4.7 ($\pm$1.2, $n = 166$) in successful first broods and 4.1 ($\pm$1.0, $n = 43$) in successful replacement clutches. Local recruitment rate from all nests steadily declined during the study period: 5.9% of the young born in 1988 ($n = 236$) bred in the study area in the consecutive year, while only 3.1% of the young born in 1991 ($n = 225$) returned to breed in 1992 (Fig. 1c). All local recruits bred in their first year after fledging, and no individual ringed as a nestling was ever observed for the first time after year 1. There was no difference in the results between the full data set and the randomly created balanced data sets for the analyses on recruitment (see Methods). We therefore report in the following only the results of the analyses using all data.

Timing of breeding

Reproductive performance

The model selection process yielded two best models, which included all tested parameters (Table 1). Model averaging showed that nest success declined from 1988 to

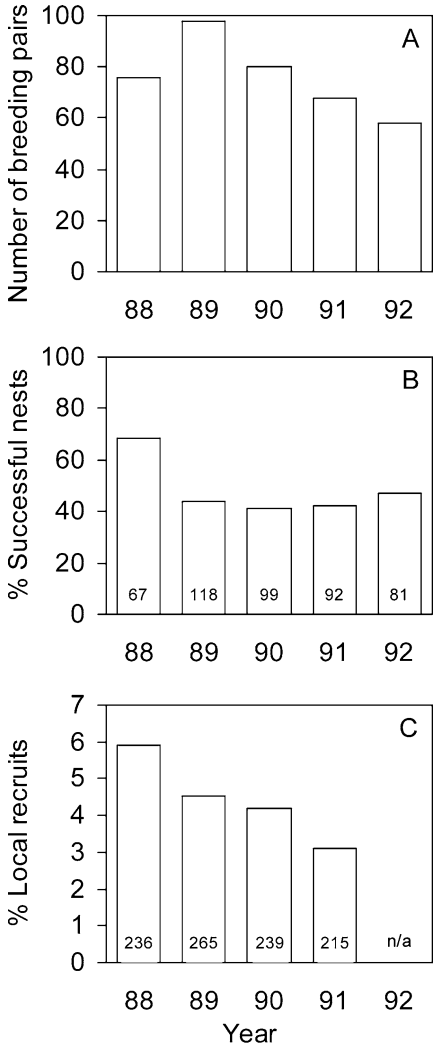

Fig. 1 Number of breeding pairs (**a**), percentage successful nests (**b**), and local recruitment rate in percentage (**c**) of the red-backed shrike from 1988 to 1992. *Numbers in bars* are sample sizes, representing total number of nests per year in **b** and total number of nestlings produced per year in **c**. No recruitment rate is available for 1992 (there were no field checks in 1993)

1992 (Table 1, year effect = -0.23 ± 0.30). Within years, early clutches were more likely to produce fledglings than late clutches (laying date effect = -0.06 ± 0.12), and nest success increased at higher altitudes (1.62 ± 0.92). There was no interaction between altitude and laying date, meaning that the positive effect of early breeding persisted over the altitudinal range of our study area. First clutches were more likely to be successful, i.e. to produce at least one fledgling, than replacement clutches (clutch sequence effect = 1.23 ± 1.74). There was an interaction between laying date and clutch sequence, indicating that early broods were only more successful than later broods in first, but not in replacement, clutches.

No model significantly explained variation in number of fledglings from successful nests as a function of variables related to the timing of breeding hypothesis.

Recruitment

The model selection process yielded four models showing that early clutches were more likely to produce at least one recruit than late clutches (laying date effect = -0.04 ± 0.10). There was no difference between first and replacement clutches, neither was there an interaction between laying date and clutch sequence. Recruitment probability declined with altitude (-1.37 ± 0.67), but increased with the number of fledglings produced (0.22 ± 0.32) and year (0.14 ± 0.22) and there was no interaction between laying date and altitude (Table 2).

Parental quality

Reproductive performance

We examined models containing age, body size and body condition of parents or subsets of these parameters. None of the models significantly explained nest success ($n = 81$) or variation in the number of fledglings of successful nests ($n = 74$).

Table 1 Factors affecting nest success in the red-backed shrike. Modelled was the probability that a nest was successful and included are only models that significantly explained probability of nest success. Of these, selected models (ΔAICc < 2) are shown for each hypothesis separately. The total number of nests (first number) and number of successful nests (second number) are given in brackets after hypotheses. ΔAICc is the difference in AICc to the best model; weight indicates the relative support of a particular model compared to the other models, with higher values indicating better support

Hypotheses	Best models	AICc	ΔAICc	Weight
Timing of breeding (321/160)	1. Laying date, year, altitude, replacement yes/no	411.14	0	0.72
	2. Laying date, year, altitude, replacement yes/no, replacement yes/no* laying date	413.00	1.86	0.28
Nest predation (249/193)	1. Jay factor	478.45	0	0.58
	2. Magpie/crow factor, jay factor	479.10	0.65	0.42
Nest site (331/192)	1. Concealment	432.49	0	0.40
	2. Concealment, year	433.10	0.61	0.30
	3. Concealment, nest height	433.10	0.59	0.30
Intraspecific density (349/193)	1. Number of neighbours, density, year	474.26	0	0.50
	2. Number of neighbours, year	475.28	1.02	0.30
	3. Distance to nearest neighbour, number of neighbours, density, year	476.13	1.88	0.20

Table 2 Factors affecting local recruitment probability in the red-backed shrike. Modelled was the probability that a nest produced at least one recruit. See Table 1 for details

Hypotheses	Best models	AICc	ΔAICc	Weight
Timing of breeding (176/41)	1. Laying date, year, altitude a.s.l., number of fledglings	186.47	0	0.33
	2. Laying date, altitude a.s.l., number of fledglings	187.14	0.32	0.28
	3. Laying date, number of fledglings	187.86	1.04	0.20
	4. Laying date, number of fledglings, year	188.00	1.15	0.19
Parental quality (58/14)	1. Male body size and condition, male age, female body condition, female age	61.18	0	0.61
	2. Male body size and condition, male age, female body condition, female age, number of fledglings	62.04	0.86	0.39
Predation (157/40)	1. Magpie/crow factor, distance to settlement, distance to forest, number of fledglings	178.21	0	0.51
	2. Jay factor, distance to settlement, distance to forest, number of fledglings	178.32	0.11	0.49
Territory quality (83/17)	1. % unmanaged areas, number of fledglings	83.30	0	0.26
	2. % unmanaged areas, number of fledglings, number of free-standing trees	83.69	0.39	0.22
	3. % unmanaged areas, number of fledglings, number of free-standing bushes	84.11	0.81	0.17
	4. % unmanaged areas, number of fledglings, number of free-standing trees and bushes	84.38	1.08	0.15
	5. % unmanaged areas, number of fledglings, number of free-standing trees, dry meadows	85.29	2.00	0.10
	6. number of fledglings, number of free-standing trees	85.29	2.00	0.10

Recruitment

Two models best explained variation in local recruitment (Table 2). The probability that a nest produced a recruit was negatively related to male body size (body size effect = -0.06 ± 0.15), male condition (-0.07 ± 0.58) and male age (-1.69 ± 0.86), but positively related to female body condition (0.22 ± 0.42) and female age (1.41 ± 0.82). Recruitment probability increased with the number of fledglings produced (0.04 ± 0.35).

Nest predation

Reproductive performance

Nest success declined with increasing numbers of territories of potential predators (magpie/crow effect = -0.11 ± 0.22; jay effect = -0.20 ± 0.33; Table 1). Distances to the nearest forests or human settlement seemed to be irrelevant for nest success. None of these variables were related to the number of fledglings produced in successful nests ($n = 193$).

Recruitment

Recruitment probability was positively related to numbers of territories of potential predators (magpie/crow effect = 0.09 ± 0.40; jay effect = 0.04 ± 0.31; Table 2) as well as to the distances to the nearest settlement (0.001 ± 0.02) and forest (0.08 ± 0.02) and to the number of fledglings produced (0.25 ± 0.43).

Nest site selection

Reproductive performance

According to our prediction that nest success is highest at an intermediate nest height (see Introduction), we included an additional quadratic term for nest height in the models. Nest success was higher for well-camouflaged nests (low values for "nest concealment") than for less concealed nests (-0.25 ± 0.24). One of the three best models also included nest height (0.01 ± 0.23), while another reflected the declining nest success over the years (-0.03 ± 0.16) (Table 1).

Only one model ($n = 192$) significantly related the number of fledglings from successful nests to variables representing the nest site selection hypothesis. When successful, more young fledged from highly camouflaged nests than from more visible nests (camouflage effect = -0.03 ± 0.02), while year had a slightly negative effect on the number of fledglings (-0.1 ± 0.02). Thus, nest concealment seems to play an important role for red-backed shrike reproductive performance.

Territory quality

Reproductive performance

Neither percentage cover of intensively managed meadows, of dry meadows, of arable and unmanaged areas, length of hedges, nor the number of free-standing bushes and of trees was significantly related to nest success ($n = 105$). Similarly, neither variable significantly affected the number of fledglings from successful nests ($n = 55$).

Recruitment

Six models were selected to explain recruitment probability (Table 2). The likelihood that a nest produced a recruit was enhanced in territories with more free-standing trees (0.04 ± 0.17) and bushes (0.47 ± 0.65), as well as in territories encompassing a larger proportion of dry meadows (0.04 ± 0.33). On the other hand, the percentage of unmanaged areas negatively affected local recruitment rate (-4.74 ± 1.71). Again, recruitment

probability was positively related to the number of fledglings (0.49 ± 0.55).

Intraspecific density

Reproductive performance

High numbers of conspecific territories within 150 m of a nest (−0.14 ± 0.25) and high population density (−0.01 ± 0.09) reduced the probability of a nest fledging young; accordingly, nest success increased with distance to the nearest red-backed shrike nest (0.0002 ± 0.02). Again, nest success declined over the years (−0.28 ± 0.33) (Table 1). None of the measures of intraspecific density affected the number of young fledged from successful nests ($n = 216$).

Recruitment

Population density did not significantly affect recruitment probability ($n = 208$ nests, 43 of which produced at least one recruit).

Weather

Reproductive performance

No model significantly related nest success to PCA factors combining temperature or rainfall variables, neither in the egg ($n = 335$) nor the nestling stage ($n = 252$). Further, no model significantly related temperature or rainfall variables to the number of fledglings in successful nests ($n = 123$), again neither if weather conditions during the egg nor the nestling stage were considered. Weather conditions did not, therefore, seem to influence reproductive performance.

Recruitment

There was no significant relationship between weather variables and recruitment probability ($n = 203$ nests, 43 of which produced at least one recruit).

Individual quality (local recruitment only)

No model significantly explained the probability that a fledgling would return to breed in the study area as a function of its body condition or its body size ($n = 176$ fledglings, 32 of which became recruits).

Full models

Reproductive performance

Variables that had been shown to influence nest success in the single-hypothesis tests (see Table 1) were jointly added to one model from which the best (sub)model was selected, again using AICc. The model selection process yielded one best model ($n = 311$ nests, 185 of which were successful); for all other models ΔAICc was >10. This final model contained laying date (−0.05 ± 0.01, Fig. 2a), year (−0.18 ± 0.1), nest concealment (−0.20 ± 0.06, Fig. 2b), the number of red-backed shrike territories within 150 m of a nest (−0.13 ± 0.07, Fig. 2c), and a weak effect of clutch sequence (replacement clutch yes/no: −0.15 ± 0.22, Fig. 2a–c). Selection of the nest site with respect to nest concealment, local density of conspecifics, and timing of clutch initiation therefore seem to be the determining factors of nest success in the red-backed shrike. The number of young that fledged from successful nests was solely influenced by nest concealment (see above), so no further analyses could be done.

Recruitment

The model selection process yielded six models with ΔAICcTable 3). All of these models confirmed the negative effect of the percentage of unmanaged land within a territory (−13.4 ± 0.1.94, Fig. 3) and the positive influence of number of fledglings (1.67 ± 0.56, Fig. 3) on recruitment probability shown above. Some of the selected models showed the negative impact of altitude (−0.07 ± 0.24) and the positive effect of free-standing trees (0.26 ± 0.19) and bushes (1.46 ± 0.55) on local recruitment rate as found in the single-hypothesis tests. Territory quality, therefore, seems to be of prime importance for the production of local recruits in the red-backed shrike.

Discussion

Reproductive performance of the red-backed shrike appears to be affected by ecological and social conditions related to timing of breeding, nest site selection and intraspecific density. Nest success, rather than number of fledglings per successful nest, seems to be the critical component of reproductive performance in the red-backed shrike, because most factors influencing reproductive performance did so at the level of nest success rather than the number of fledglings per successful nest. With respect to local recruitment, the only factors that appeared to be important were territory quality, altitude, and the number of fledglings produced per nest. In the following discussion, emphasis is given to factors that were found to be important in both the single-hypothesis tests and the full model analysis, whereas effects suggested to be influential only in the single-hypothesis tests are considered less important.

Timing of breeding, and parental and territory quality

Breeding early in the season has been found to be associated with a high reproductive output in many bird

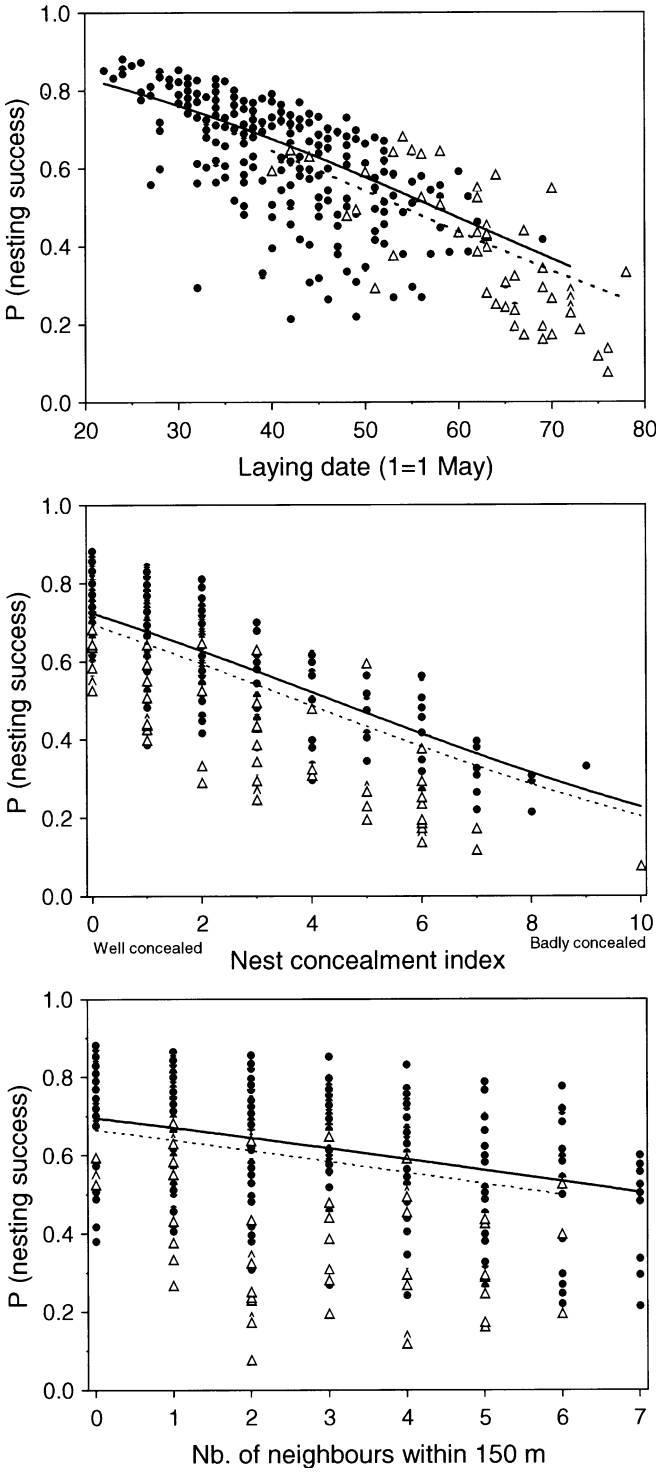

Fig. 2 Probability of nest success in relation to: (**a**) laying date, (**b**) nest concealment and (**c**) number of neighbours within 150 m of the nest in first (*solid circle*, *solid line*) and replacement clutches (*open triangle*, *dashed line*). Model results of a logistic regression including the variables (1) "laying date", (2) "nest concealment index", and (3) "number of neighbours within 150 m around the nest" and the factor "first/replacement clutch". Symbols represent the predicted values for nest success from the full model, calculated with the observed values for variables 1–3 for 311 nests. The lines indicate the predicted nest success with the following variables set to mean observed values: (**a**) variables 2 and 3, (**b**) variables 1 and 3, and (**c**) variables 1 and 2. Year effect was ignored

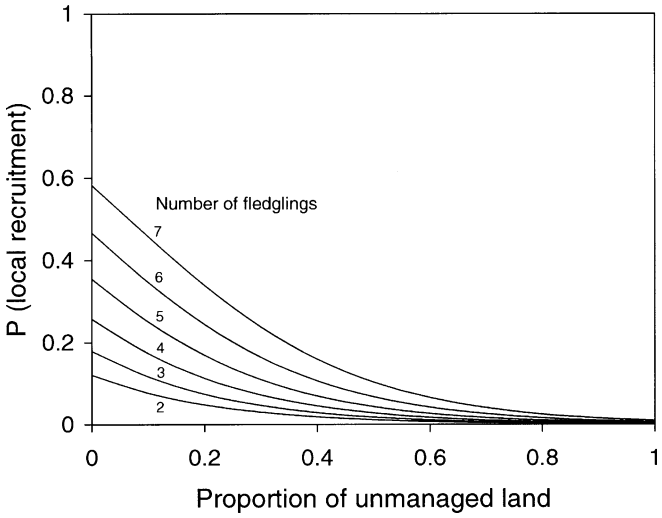

Fig. 3 Probability of local recruitment versus the proportion of unmanaged land and the number of fledglings per nest. Model result of a logistic regression including the variables: (1) "number of fledged young" and (2) "proportion of unmanaged land" within each territory

species (e.g. Verhulst et al. 1995; Naef-Daenzer et al. 2001; Schiegg et al. 2002). An early onset of breeding is assumed to increase the chances that the period of highest food demand of the brood coincides with the peak of food availability and, in addition, to allow more time for production and development of offspring of either the first or following broods. In our study, the timing-of-breeding hypothesis was clearly supported, in that the probability of success was higher for early rather than late nests and for first rather than replacement clutches. The interaction between laying date and clutch sequence indicated that early clutches were more successful in first broods only, whereas laying date did not influence the success of replacement clutches. These results were consistent in the single-hypothesis tests and in the full model analyses, while an effect of altitude and the interaction between laying date and clutch sequence was apparent only in the single-hypothesis test. Hence, timing of breeding is of central importance to the reproductive performance of the red-backed shrike in our study population, as well as the other factors discussed below.

Earlier studies have suggested that increased reproductive performance of early-laying females is not due to laying date per se, but is mediated via factors such as female and/or territory quality. Theoretical, experimental and empirical studies have shown that females in good condition can breed early in the season and can have larger clutches as well (see Price 1998 for a recent review), resulting in greater fitness compared to females in poor condition (Gorman and Nager 2003; Reynolds et al. 2003). In turn, Meijer and Drent (1999) suggested, by means of a meta-analysis, that neither the start of egg laying nor the number or quality of eggs are directly related to the energetics of the laying female. This is in

Table 3 Full models of local recruitment probability in the red-backed shrike. Modeled was the probability that a nest produced at least one recruit. See Table 1 for details

Best models	AICc	ΔAICc	Weight
1. % unmanaged areas, number of fledglings	83.30	0	0.24
2. % unmanaged areas, number of fledglings, number of free-standing trees	83.69	0.39	0.19
3. % unmanaged areas, number of fledglings, altitude a.s.l.	84.02	0.72	0.16
4. % unmanaged areas, number of fledglings, number of free-standing bushes	84.11	0.81	0.16
5. % unmanaged areas, number of fledglings, number of free-standing trees and bushes	84.38	1.08	0.14
6. % unmanaged areas, number of fledglings, number of free-standing trees, altitude a.s.l.	84.85	1.55	0.11

line with the findings of this study, suggesting that timing of breeding, but not female quality, is important for reproductive performance. It is possible that the variables used here did not adequately measure female quality, although many studies on birds have found body size (e.g. Møller et al. 2003) and body condition (body mass; Wendeln and Becker 1999) to reflect individual quality. Interestingly, the age of parents did not influence reproductive performance either, despite many studies indicating reproductive performance to increase with age (e.g. Newton 1989; Saether 1990). Improvements in reproductive performance with age may be attributed to advantages in access to high-quality territories for older over younger birds rather than to increased foraging skills, breeding experience or local familiarity (Pärt 2001), but we failed to find consistent effects of territory quality or age on reproductive performance. Again, one explanation for this pattern may be that the habitat variables used do not adequately reflect habitat quality for red-backed shrikes. This is rather unlikely, however, because other studies have demonstrated that low-intensity farming and high availability of hedges are key components in red-backed shrike habitats (Glutz von Blotzheim and Bauer 1993; Leugger-Eggimann 1997; M. Müller et al. unpublished data). A more likely explanation is that the study area generally offers high-quality habitat, as indicated by the very high population density of up to 5.4 breeding pairs per 10 ha versus average densities of two to four breeding pairs per 10 ha in other parts of Switzerland (Müller and Leugger 1998) and Europe (Glutz von Blotzheim and Bauer 1993). Thus, small differences in quality among territories, if they existed at all in our study area, do not seem to be sufficient to result in differential reproductive performance among age classes.

So, if reproductive performance depends so much on timing of breeding, why don't all individuals breed early? One explanation may be that the birds indeed breed as early as possible, but that intrinsic factors not considered here influence egg laying. For example, it is known that divorce between seasons may result in a delayed onset of breeding in the following year (Schiegg et al. 2002), even if both individuals forming the new pair already have breeding experience with another partner. Such effects are independent of age and/or individual quality, which may explain the lack of relationship between reproductive performance and age as well as parental quality.

Nest predation and nest site selection

Our results suggest that nest concealment is an important factor for the probability of nest success in red-backed shrikes. Well hidden nests were significantly more likely to fledge young than less camouflaged nests. It is also noteworthy to point out that nest concealment was the only factor affecting the number of fledglings from successful nests. Nest height above ground was not consistently related to nest success, corroborating earlier findings (Tryjanowski et al. 2000). Substrate type of the nest carrier was not a significant predictor of nest success either, agreeing with Farkas et al. (1997), but not with Jakober and Stauber (1981, 1987) or Tryjanowski et al. (2000).

Most nest losses could be clearly assigned to some predation event. Nest success declined with increasing numbers of corvid territories in the study area, but this effect vanished in the full model analysis. Because variation within our measures of predation pressure only reflected annual fluctuations in the density of potential predators, our results may be confounded by annual variations of unknown source affecting nest success. Yet, whatever the precise nature of nest predators and their impact were in our study, predation pressure exerted by these predators shapes nest site selection of individuals (see also Roos and Pärt 2004), as indicated by the clear relationship between nest concealment and reproductive success discussed above. This study, therefore, provides additional evidence for the importance of nest predation for reproductive performance of individuals and, ultimately, for life history evolution of species (Martin 1995).

Intraspecific density

Density dependence is an important mechanism in the regulation of populations. Competition and predation have been proposed as possible sources of density dependence (Hixon et al. 2002). In birds, density dependence via competition can lead to reduced fecundity (Rosenzweig 1991) and survival (Altwegg et al. 2003). In our study, the number of red-backed shrike territories within 150 m of a nest, a measure of local density, was the only variable consistently resulting in low nest success (single-hypothesis test and full model analyses), providing an example of density-

dependent population regulation acting via fecundity, presumably mediated through intraspecific competition. Similar findings have been reported in many studies on birds (Newton 1998 and studies therein). On the other hand, red-backed shrikes are known to depredate nests of conspecifics (personal observation), so that the observed relationship between local density and red-backed shrike nest success may be the result of intraspecific predation rather than competition. Predation by avian species other than red-backed shrikes appeared to be of minor importance (see above), while the role of other predators could not be satisfactorily assessed in this study. Nevertheless, the red-backed shrike may provide an example of how competition and predation, both acting at the intraspecific level, interact to cause density-dependent population regulation (Whitfield 2003).

Weather

We found no evidence that weather conditions affected reproductive performance of the red-backed shrike. This was surprising, because weather effects on reproduction have been shown in a variety of bird species (Krüger 2002; Rodriguez and Bustamante 2003). In addition, our study was conducted at an altitude where the time window suitable for breeding is considerably narrower than in the lowlands, thereby increasing the pressure for pairs to start breeding shortly after arrival on their sub-alpine breeding grounds. Since cold spells, accompanied by rain- and snowfall, are not uncommon in the Swiss Alps throughout the breeding period (Glutz von Blotzheim 1990, own observation), early broods may fail completely or may suffer from reduced food availability due to delayed vegetation development following inclement weather. However, the lack of any weather effects on reproductive performance of the red-backed shrike in the egg and nestling stages suggests that individuals breeding at high altitudes have developed specific strategies to cope with unpredictable weather events. Behavioural adaptations resulting in better nest insulation and increased brood care have been reported for garden warblers (*Sylvia borin*, Boddaert) breeding at high altitudes compared to lowland breeders (Widmer 1993), while evidence for physiological adaptations is generally missing (Widmer 1999).

Local recruitment

Three main factors turned out to be important predictors in both the single hypothesis and the full model analyses, the first one being the number of fledglings produced per nest. If more fledglings were available to begin with, it was more likely that one of these would become a local recruit. An increase of one fledgling resulted in a 59.1% increase in the odds of a nest producing a recruit (Fig. 3). Similar positive relationships between numbers of fledglings and recruits have been found in some studies on birds (Brommer et al. 1998), while others have indicated that large clutches produce fewer recruits (Van Noordwijk and van Balen 1988). The second factor influencing local recruitment probability was territory quality, mainly the percentage area of a territory covered by unmanaged land. Recruitment probability was reduced with increasing proportion of unmanaged land. This result may seem counterintuitive at first, because unmanaged land is expected to have higher invertebrate abundances than managed areas. On the other hand, it is known that hunting success of different shrike species is highest when the ground vegetation is not too dense and/or tall (Rehsteiner 2001). We therefore argue that the negative influence of unmanaged land on local recruitment probability reflects the difficulties the fledglings have finding enough food. Fledglings, in particular, may be affected by unfavourable habitat because they are less experienced in foraging and avoiding predators than adults. Finally, altitude negatively affected recruitment probability, which may be attributed to a delayed onset of breeding at higher altitudes resulting in less time for the fledglings to attain the physical condition required for successful migration.

We found no clear evidence that further ecological or social factors influence the probability of local recruitment. Seasonal declines in recruitment probability, as suggested here in the single-hypothesis analysis, are usually attributed to declining food availability and/or to increasing predation pressure (Blums et al. 2002). In our sub-alpine study area, food availability increases, rather than decreases, during the short breeding period (lasting 49–61 days, own unpublished data) of the red-backed shrike, given the frequent cold spells in the sub-alpine environment early in the breeding season and the increasing temperature until mid-summer. Predation pressure is likely to increase with season, because most predators will have grown young to care for, with a high food demand, but factors used here to estimate predation pressure (PCA factors reflecting corvid densities) did not influence recruitment probability.

Conclusions

The reproductive performance of the red-backed shrike appears to depend on a combination of factors, the most influential ones being timing of breeding, nest site selection and intraspecific density. In a first step, natural selection appears to act at the nest level: whether or not a nest is successful determines the potential for local recruits to be produced. In a second step, selection seems to act on brood size, as the probability of a nest producing recruits was positively related to the number of fledglings. Thus, the prime determinant of individual fitness in the red-backed shrike appears to be nest success, which in turn affects the probability of local recruitment.

This study highlights the importance of including many potentially influential factors to investigate their joint and relative impact on fitness (c.f. Krüger 2002). While experimental studies provide unequivocal insight into causal relationships among variables, they are restricted to inferences drawn from a limited number of predictor variables only. In contrast, multivariate approaches, such as the one applied in this study, allow the assessment of the importance of many variables acting in concert on response variables of interest. Such integrative approaches are needed to understand how natural selection acts on different life-history traits and strategies in complex environments.

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